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ARAUCARIOPITYS, A NEW GENUS OF ARAUCARIANS

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(WITH PLATES XXVIII-XXX)

Among the coniferous remains discovered in the Cretaceous deposits of the Androvette pit, Kreischerville, Staten Island, are certain leafless twigs, bearing spirally arranged scars. In most cases the twigs in question are decorticated as well as deprived of their appendages; in fact, in all the best-preserved material this is the case. An examination of the internal structure of these remains showed that they were Araucarian in their affinities; but possessed deciduous shoots, similar to those occurring in *Pinus*. The deciduous shoots seem to have been of seasonal duration only. The branches of the type described above were found in association with impressions of the deciduous leaf-fascicles of *Czekanowskia*, a supposed but doubtful representative of the Ginkgoales. It is not improbable that the two sorts of remains belong to each other, although it is impossible to more than infer that such is the case at the present time.

Fig. 1 represents a transverse section through a rather well-preserved stem of our species, which we propose to call ***Araucariopitys americana***, for reasons to be stated later. The lower right-hand portion of the section is in a bad state of preservation. There are two marked indentations of the surface of the decorticated stem; these mark the positions of two deciduous leafy shoots. The indentation on the extreme right of the figure occurs in the less well-preserved region, so that the topography of the relation of the deciduous shoot to the supporting axis is not clear. The indentation on the upper left-hand part of the surface of the stem corresponds to a short shoot, which is not cut axially by the plane of section. In the well-preserved part of the wood it is obvious that there is but a single annual ring present. A noteworthy feature of the wood is the presence of a tangential row of traumatic resin canals. These traumatic canals are very common

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in this species, occurring in nearly half the specimens in our possession. It would thus appear that the species was very easily stimulated to the formation of traumatic resin ducts.

The pith is not well shown in *fig. 1* on account of the partial decay of the specimen. In *fig. 3* it appears more clearly, and it is possible to distinguish that there are certain dark areas in it, which correspond to islands or nests of sclerotic cells, similar to those which are found in the medulla of the Cretaceous genus *Brachyphyllum*. The pith is relatively large in size, exceeding in its proportions that found in living *Cupressineae*. *Fig. 3*, which was made from a section higher up in the branch than that which supplied *fig. 1*, shows on the upper right-hand side the presence of a small portion of the cortex and bark *in situ*. In the cortex are present, although this feature is not apparent in the figure, the same islands or nests of sclerotic tissue which are found in the medulla.

Fig. 2 shows the cross-section of another less well-preserved stem, which has lost part of its woody tissues, but still retains a considerable portion of its bark. The apparent cracks in the wood represent rows of resin canals, which the magnification is not sufficient to make apparent. *Fig. 4* illustrates a part of the same stem as that shown in *figs. 1* and *3*, under a higher magnification. The row of traumatic resin canals can be particularly well made out here and also the sclerifications, which appear as dark spots in the pith.

Fig. 5 shows a portion of the section figured in *fig. 1*, under a considerable degree of magnification. The absence of resiniferous cells, such as are a feature of the wood of the *Cupressineae*, can be made out. A number of rounded cavities appear in the wood, which are the traumatic resin canals. By their rounded contour, they more nearly resemble those of the *Abietineae* in aspect than those of any other of the Cretaceous *Araucarineae* which we have studied. The resin canals are surrounded by one or more layers of parenchyma cells, which appear to be devoid of contents. Often there is present in the lumen of the canals themselves a dark-hued substance, which is in all probability a fossil gum or mucilage, since it is not soluble in any of the numerous solvents of resin used hot in the process of preparing the material for sectioning. This substance apparently corresponds to that described as present in the traumatic resin

canals of other Araucarian lignites from various levels of the Cretaceous.²

Fig. 6 shows a tangential longitudinal section of the wood of our species, through the region of the traumatic resin canals. It is to be noted that these are more numerous than is the case with normal resin canals, and are somewhat constricted at intervals, both features to be found in the wound-canals of the Abietineae. In the region of disturbance shown in *fig. 6*, the rays vary greatly in height, being composed of from one to many cells. *Fig. 7* shows the left-hand portion of *fig. 6*, more highly magnified. In this figure the end walls of the ray cells, which appear in face view, are strongly pitted, a feature found in no other living or fossil Araucarian, which has been described, but very characteristic of the Abietineae. Both the end and horizontal walls of the ray cells in *Agathis* and *Araucaria*, for example, are smooth, and this statement equally holds for the numerous species of Mesozoic Araucarians which it has been possible to study in the Androvetta deposits. Our present species differs, then, from all other Araucarians, living or extinct, in the presence of abundant pitting on the terminal and horizontal walls of the cells of its medullary rays. The cells constituting the rays are entirely parenchymatous and there are no tracheidal cells present, such as occur in the rays of certain species of living Abietineae. *Fig. 9* shows with sufficient clearness the strongly pitted horizontal wall of the ray cells in our species.

In *fig. 8* is seen a longitudinal approximately radial section of the wood in *Araucariopitys*. The magnification is scarcely sufficient to show the araucarian radial pitting of the tracheids. This section shows very well, however, the constriction of the traumatic resin canals at intervals, which Professor PENHALLOW, in the case of the traumatic and normal resin canals of certain Abietineae, has interpreted as an indication of the derivation of the continuous system of resin canals, present, for example, in *Pinus*, from the union with each other of a number of originally isolated resin spaces or cysts.³ This view, as will be shown on another occasion, can scarcely be accepted.

² JEFFREY, E. C., The wound-reactions of *Brachyphyllum*. *Annals of Botany* 20:383-394. pls. 27, 28. 1906.

³ PENHALLOW, D. P., The anatomy of the Coniferales. *Amer. Nat.* 38:243 ff. 1904.

Fig. 10 shows the structure of the pith in our species. It will be seen that it is traversed at intervals by diaphragms of sclerenchymatous cells, which strongly recall those to be found in *Abies*, *Picea*, and certain hard pines. The stone cells are arranged in longitudinal rows, as if they had been formed by the transverse divisions of a horizontal series of mother cells, as has been described in certain *Calamites* and *Equiseta*. *Fig. 11* illustrates the character of the radial pitting in our species. It will be seen by examination of the pits on the left of the figure that some of them are in intimate contact and are mutually flattened, in the manner characteristic of the radial pitting of *Araucarioxylon* Kraus. There is a clear distinction from the typical condition in *Araucarioxylon*, however, in the fact that not all the pits are mutually flattened, but some of them are rounded in contour, as in the wood of the *Abietineae*. The pitting in our species is thus transitional between the types characteristic of *Araucarioxylon* and *Pityoxylon* or *Cedroxylon*. In the general memoir on the Conifers of the Androvetta Cretaceous deposits, it has been proposed that woods of a type transitional between the modes of radial pitting found in the *Araucarineae* and *Abietineae* should come under a new genus *Brachyoxylon*, taking the wood of the genus *Brachyphyllum* as the type. Our present species, however, can scarcely be put under *Brachyoxylon*, since in the latter the terminal and horizontal walls of the ray cells are smooth as in the living *Agathis* and *Araucaria* and their near allies of the Mesozoic. In the species under discussion, by contrast the terminal and horizontal walls of the ray cells are both strongly pitted, as is typically the case in the *Abietineae*. If other species of lignites are subsequently discovered which agree with that under discussion in their essential features, it will probably be well to establish the name *Araucariopityoxylon* or some convenient abbreviation of it for their reception. So long as the type is represented by a single lignitic species, however, the name *Araucariopitys* will suffice both for the branches and the wood. On the other hand, if it is proved subsequently that *Araucariopitys* represents the branches of *Czekanowskia*, as we strongly suspect to be the case, both names will have to be merged in *Czekanowskia*.

In *fig. 12* is shown a highly magnified view of the radial pitting of the species under discussion. The field is so chosen as to include

mainly tracheids, showing the araucarian type of pitting. Occasionally a tracheid may be found in longitudinal sections of our species, broad enough in its terminal region to accomodate a double row of pits, in which case the phenomenon of alternation as well as flattening may be observed, although even the biseriate pits are sometimes found to be opposite as in the Abietineae. It may be questioned by the reader whether the evidence afforded by the pitting alone is strong enough to decide the Araucarian affinities of the genus we have been describing. We have no inclination to deny the propriety of such a doubt, but we consider it to be removed by the fact that the large number of presumably transitional Araucarians found in the form of well-preserved leafy branches in the Androvetta deposits were accompanied by numerous associated cone-scales, which, where they did not obviously belong to *Pinus*, were also Araucarian and of a transitional type of organization. For a full discussion of this matter the reader is referred to the joint memoir already cited.

Fig. 13 illustrates the short shoot of *Araucariopitys* as seen in tangential section under low magnification. The brachyblast is present in the upper part of the field. Below it there is a scarcely perceptible disturbance in the arrangement of the tracheids, indicating the position of the foliar trace, to which the short shoot is axillary. It is apparent, from the topography of the tangential section of the wood, that the axillating leaf was better developed in *Araucariopitys* than is generally the case in *Pinus*, where the subtending foliar organ is usually obsolete or has degenerated into a mere scale. There are of course in *Pinus* certain exceptions to this statement in the case of seedlings and the shoots growing out of injured branches. In *fig. 14* is represented a more highly magnified view of the section of the same short shoot shown in *fig. 13*. *Fig. 15* represents a radial section through the axis of the short shoot, which at the same time includes a part of the woody cylinder and the pith of the parent axis. In *fig. 16* is seen a transverse section through the main axis at the level of exit of one of the brachyblasts. It is easy to determine from the sections just described that the woody cylinder of the short shoot projects little if at all beyond the surface of the wood of the main axis. *Figs. 12-17* have all been made from another specimen than that which furnished *figs. 1, 3, 4, 5*. *Fig. 17* presents a somewhat magni-

fied image of the transverse section of the axillating leaf trace as seen in longitudinal section of the axis. There is obviously a considerable disturbance in the arrangement of the tracheids of the axis.

All the available specimens of our fossil showing the bark in place are unfortunately badly preserved. They confirm the conclusion, however, that *Araucariopitys* possessed deciduous shoots comparable with those of living pines and at the same time was an araucarian Conifer. The condition of preservation in the corticated specimens makes it possible to observe that the deciduous shoots have already fallen in branches which show but a single annual ring and are subtended by definite absciss layers occurring in the outer cortex. There are no peridermoid tissues present except in the limited areas immediately opposite the deciduous shoots.

It will be obvious to the reader that in the coniferous branches to which we have assigned the name *Araucariopitys*, there are features present which combine in a remarkable degree the anatomical characteristics of both the *Abietineae* and *Araucarineae*. The radial pitting of the tracheids, for example, as has been shown above, is clearly transitional between the two orders. The rays tend more strongly to the abietineous side. The wound-reactions of our Conifer are more like those of the *Abietineae* than are those of any other known *Araucarian*. Finally, the genus was characterized by the possession of deciduous shoots. It will be obvious from the enumeration of the features that in the species under discussion we have a strong araucarian endowment with a nearer approach to abietineous structure than has been found in any *Araucarian* living or extinct. Since this is the case, the name *Araucariopitys*, etymologically significant of the double affinities, seems appropriate.

CONCLUSIONS

It appears from the description given above that there are present in the Cretaceous deposits of Kreischerville, Staten Island, N. Y., certain branches with deciduous lateral shoots, resembling in their relation to the axis the brachyblasts in the abietineous genus *Pinus*. Further, it is apparent that in spite of the possession of deciduous shoots, the branches in question belong to an araucariaian Conifer of archaic type, as is shown by their anatomical structure. The wood

of these shoots presented the wound-reactions of the Abietineae, radial pitting of the tracheids transitional between the Abietineae and Araucarineae, and the ray structure of the Abietineae. It is moreover probable that leafy shoots known under the generic appellation of *Czekanowskia* belonged to our species, since the former occur in impressions in association with these remains.

It appears clear that in *Araucariopitys* we have to do with a genus transitional in its characters to a marked degree and nearer to the Abietineae than any other known araucarian genus living or extinct. The existence in the Mesozoic of types like *Araucariopitys*, *Brachyphyllum*, *Geinitzia*, etc., combining in so many ways abietineous and araucarian characters, does not make it easy to accept as correct the position recently adopted by Professor SEWARD⁴ that the Araucarineae are distinct from, and without immediate affiliations with, the other coniferous orders. It is indeed not difficult to show that the aberrant forms which represent the Araucarineae in the existent flora are sufficiently different from the Abietineae and most of the other coniferous families; but such a conclusion cannot now be projected into the past, in the face of our recent fuller knowledge of the structural features of the araucarian flora of the Mesozoic.

Since it must apparently be admitted that in the Mesozoic the abietineous and araucarian Conifers were not so clearly separated from each other as the living representatives of those families are, the question arises, which of these two admittedly ancient families lies nearer to the ancestral stock? Professor SEWARD and others have argued, from the rich luxuriance of the araucarian flora in the Cretaceous and even earlier periods of the Mesozoic (a luxuriance which our own studies, as described in the monograph already referred to, only serve to emphasize), as compared with the comparative poverty of the abietineous display, for the superior antiquity of the araucarian Conifers. Such an argument appears, however, to be fallacious. It would be just as logical to assume that at any given period the richly developed crown of a forest tree was its oldest portion. All the evidence goes to show that the Araucarians were indeed the crown of the coniferous genealogical tree during the Mesozoic, but

⁴ SEWARD, A. C., and FORD, S. O., The Araucarieae, recent and extinct. Phil. Trans. Roy. Soc. London B. 198:305-411. pls. 23, 24. 1906.

in the changes which ushered in the Tertiary the crown was almost completely destroyed and that a lower more ancient and overshadowed branch, the Abietineae, became a new "leader" and developed luxuriantly.

Concerning the derivation of the Araucarineae from the Abietineae in the beginning of the Mesozoic period, evidence has rapidly accumulated of late. Reference has been made above to the striking abietineous characteristics of the older Araucarians. It has been pointed out that the wound-reactions of the older Araucarineae are a strong indication of their abietineous derivation. Further, although the older Araucarians show striking transitions in their pitting toward the Abietineae, even the most archaic structurally known abietineous type, *Prepinus*, shows no tendency whatever toward the araucarian form of bordered pit. In the case of *Prepinus* just referred to, we are moreover forced to the conclusion that we have to do with an extremely ancient coniferous type, since the foliar bundles show an abundant development of true centripetal wood as distinguished from mere transfusion tissue. Further, the leaf traces are completely surrounded by a complicated double sheath of transfusion tissue, which has its exact counterpart in certain Cordaites but not elsewhere. *Prepinus*, in other words, manifests a nearer affinity to the ancestral Gymnosperms than any other known Conifer, and at the same time is clearly related to the Cretaceous species of *Pinus*, as is shown in the article cited. An additional argument for the superior antiquity of the Abietineae is afforded by the morphology of the female cone. It is true that Professor SEWARD, in the memoir cited above, has questioned whether the same morphological explanation can be offered of the female cone in the Abietineae and Araucarineae, in view of what he considers to be the slight degree of relationship between them. That the two families must be regarded as somewhat nearly allied we have tried to show above. If it be admitted that they are closely connected it follows that a common explanation of their ovulate strobilus should be possible. If we accept the generally approved explanation of the double cone-scale present in the female cone of the Abietineae, namely, that the upper ovuliferous scale is an axillary structure of shoot value subtending the sterile bract, then we are almost driven to regard the single cone-scale of the Araucarineae with

its *double* system of bundles as having resulted from the *fusion* of the two organs present in the Abietineae. If this be granted, it is not easy to deny to the Abietineae a superior antiquity.

SUMMARY

1. *Araucariopitys* is an araucarian Conifer found in the Middle Cretaceous Clays of Staten Island, N. Y.

2. Its structure and its association with impressions of the leaf-fascicles of *Czekanowskia* make it possible that it constitutes the branches of that genus, which in such a case cannot be regarded as belonging to the Ginkgoales.

3. *Araucariopitys* was characterized by the possession of deciduous shoots, which apparently persisted for a single year; by the characteristic radial pitting of its tracheids, transitional between true araucarian pitting and that found in the Abietineae; by rays differing from the araucarian type and approximating the abietineous type; by the formation of traumatic resin canals closely resembling those found in the Abietineae.

4. *Araucariopitys*, although unquestionably araucarian, was nearer in structure to the Abietineae than any other known araucarian genus living or extinct, and has been named in accordance with this fact.

5. *Araucariopitys* supplies additional evidence for the derivation of the Araucarineae from the Abietineae.

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EXPLANATION OF PLATES XXVIII-XXX

PLATE XXVIII

FIG. 1. Transverse section of stem of *Araucariopitys americana*. $\times 30$.

FIG. 2. Transverse section of another specimen of the same. $\times 18$.

FIG. 3. Transverse section of stem of *Araucariopitys americana* from the same specimen as *fig. 1*. $\times 24$.

FIG. 4. Transverse section of part of the same. $\times 40$.

FIG. 5. Transverse section of the same to show the traumatic resin canals. $\times 180$.

PLATE XXIX

FIG. 6. Tangential longitudinal section of *Araucariopitys americana*. $\times 100$.

FIG. 7. Tangential section of the same. $\times 180$.

FIG. 8. Longitudinal approximately radial section of the same. $\times 40$.

FIG. 9. Radial section of the same, showing structure of the ray. $\times 500$.

FIG. 10. Section of the medulla of the same. $\times 40$.

FIG. 11. Longitudinal radial section of the same. $\times 180$.

PLATE XXX

FIG. 12. Longitudinal section of the tracheids of the same to show Araucarioxylon pitting. $\times 500$.

FIG. 13. Tangential section of main axis of Araucariopitys, showing the presence of a short shoot and its axillating leaf trace. $\times 25$.

FIG. 14. The short shoot of the same. $\times 40$.

FIG. 15. Radial section through the deciduous shoot of the same. $\times 40$.

FIG. 16. Transverse section of wood of Araucariopitys, showing the base of the deciduous shoot in longitudinal section. $\times 40$.

FIG. 17. Tangential section of wood of Araucariopitys, showing the trace of the axillating leaf in transverse section.



JEFFREY on ARAUCARIOPITYS



